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THE HELIOTROPISM OF HYDRA.[1]

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I. *Introductory.*—Every observer of Hydra is familiar with the fact that the animal possesses considerable power of locomotion, and under certain circumstances may creep restlessly about the aquarium; it is not so generally known that its wanderings, which on superficial examination seem vague and meaningless, are in reality directed towards a definite end, and play an important part in the life of the animal. Trembley observed as long ago as 1791 that the movements of *Hydra viridis* show a definite relation to the source of light (heliotropism), the animal manifesting a marked tendency to collect on the illuminated side of the aquarium. Although this heliotropism is now well known, it has not received the attention it deserves; as far as I know, indeed, nothing has been added to Trembley's account by later observers. I find no mention of the subject in any of the more recent papers on heliotropism, except in Loeb's very interesting work,[2] and this gives no more than a brief review of Trembley's results. The subject is, however, one of considerable interest for several reasons. Hydra is not known to possess any kind of differentiated visual apparatus; the animals can be kept under observation for a long time and their behavior closely studied; the comparison of *H. fusca* with *H. viridis* enables us to determine how the

[1] Read before the American Morphological Society, December, 1890.

[2] Heliotropismus der Thiere. Würzburg, 1890.

movements are affected by the presence of chlorophyll; on account of their slowness, the movements may be accurately followed step by step.

Although the observations recorded in the following pages have occupied my attention at intervals for several years, they are still far from exhaustive, and I offer them only as a beginning. They indicate, however, that the purpose of the creeping movements and the stimuli that call them forth have not hitherto received any satisfactory explanation, and that a number of very interesting physiological questions connected with them have in consequence been overlooked. Since the heliotropic movements are complicated by other actions, I will first describe the general character of the movements as a whole.

II. *General Character of the Movements.*—Marshall has given a very good account of the mode of locomotion of Hydra,[3] though he makes no attempt at an accurate analysis of the movements, and does not mention heliotropism. I shall therefore treat only of the general character of the movements. The following account applies both to *H. viridis* and to *H. fusca*, unless otherwise stated. In a light of moderate intensity (in a north room) the animals, after wandering more or less irregularly about, gradually collect on the side turned towards the window, usually not far from the surface of the water, though here and there a straggler lags in the background or along the sides of the aquarium. The movements then become less active; the animals may remain for a considerable time with only slight changes of position, and, if the food be abundant, rapidly increase in number by growth and budding. It appears, therefore, that in moderate daylight Hydra is positively heliotropic, and its behavior is the same with lamplight, even if it be of very low intensity. If the intensity of the light be increased, a point is ultimately reached at which the action is reversed and the animals move away from the light (*i.e.*, the heliotropism becomes negative), though this action is less striking in its results than the advance movement, since the animals do not collect on the side opposite to the light, but move into the shadow of leaves, etc., or seek the

[3] *Zeitschrift für Wiss. Zoologie*, XXXVII., 1882.

bottom. It is, however, difficult to determine the precise character of the negative heliotropism, since it only occurs at an intensity that is unfavorable to the general condition of the aquarium, and thus indirectly injures the Hydras.

Up to this point there is no essential difference in the behavior of the two species, although, as many observers of Hydra have pointed out, the movements of *H. viridis* are more rapid than those of *H. fusca*, so that the former species almost invariably leads the march towards the light. If now the aquarium be allowed to stand for a long time undisturbed (the water remaining unchanged, but maintained at a constant level), until the food supply of Daphnia, Cypris, etc., becomes scanty, a very interesting series of movements may be observed in *H. fusca.* (They are only occasionally performed by *H. viridis*, and never, so far as I have observed, with the same regularity as in the former species.) After a prolonged stay near the surface the animal detaches itself from the the glass, and with tentacles widely outstretched sinks slowly to the bottom, often floating for a time at the surface before the descent. Arrived at the bottom, it slowly crawls once more to the light side, gradually, and with many deviations from the straight course, reascends to the surface, ultimately sinks again to the bottom, and so on. Thus the movements pass through a cycle, extremely variable in its details, but on the whole maintaining the character of a slow and regular rotation. The duration of the cycle is extremely variable; it may be only one or two days, or it may be as many weeks.[4]

What is the use of these movements, and by what stimuli are they called forth?

III. *Purpose and Cause of the Movements.*—It appears to be commonly assumed that Hydra moves towards the source of light "for the sake of warmth,"—*i. e.*, that within suitable limits a higher temperature is more agreeable to the animal or more

[4] In order to realize the truth of this description it is necessary to have under observation a large number of individuals in a large aquarium, to which they have become thoroughly accustomed by a residence of weeks or months. Many of my observations have been made on a fraternity of Hydras from five hundred to a thousand strong, all of which had arisen in the aquarium from a group of three or four progenitors, in the course of about two months. In this fraternity the cyclical character of the movements was very marked, and the descent of the animals might be observed almost at any time.

favorable to its physiological processes. Whether the animal has any "preferences" or exercises any conscious choice is an open question; but this question aside, the assumption that it is stimulated to move towards the light by the invisible heat-rays is clearly without foundation. The light, before impinging upon the animal, must as a rule traverse a considerable thickness of water, by which the heat-rays are almost wholly absorbed, and thus rendered inoperative. Experimentally the same result is given as follows: If in the winter season an aquarium be placed close to a north window, in a warm room, the animals collect as usual on the light side, although, as shown by a thermopyle, the other sides may receive a much greater supply of heat-rays. Experiments with Bunsen flames or heated objects placed close to the aquarium and kept in a fixed position for days show no perceptible movement of the Hydras towards the source of heat, provided no luminous rays are given off from it. The most convincing evidence is afforded by the behavior of Hydras towards rays that have passed through water as compared with rays that have passed through liquids absorbing the same amount of heat but transmitting fewer light-rays. Thus it is easy to arrange an apparatus such that a group of Hydras is offered the choice between rays that have passed through water (transparent to the visible rays, but nearly impervious to heat-rays) and a strong solution of iodine which, as shown by the thermopyle, is practically the same as water in respect to the transmission of heat-rays, but absorbs a large proportion of the visible rays. Under these circumstances the Hydras invariably move in the direction of the rays that have traversed the water, thus proving that the attractive influence must be exerted by the visible rays.

It is certain, therefore, that notwithstanding their complete lack of definite visual apparatus, both species of Hydra are not only very sensitive to the visible rays, but perform definite actions in response to the stimuli afforded by them. It seems certain, also, that the heliotropism cannot have the same part to play as in the life of green plants, since it is not peculiar to the green Hydra. In this regard Hydra differs strikingly from the Protozoa, in

which, as a rule, it is only the chlorophyll-containing forms that seek the light.

The main purpose of the heliotropic movements, as I am convinced, is simply to place the animals in the position of maximum food supply, and the entire cycle of movements of which heliotropism is a factor may be explained on the same basis. The favorite and usual food of Hydra consists of various minute Crustacea,—Daphnia, Cypris, and other Entomostraca, especially the first named,—though it will readily devour insect larvæ and many other small animals. It is a well-known fact that Daphnia and related forms manifest in a high degree a heliotropism of the same character as that of Hydra,—*i. e.*, positive in moderate light, negative in strong light,—and it must result from this that so far as the movements of the two animals are determined by light the tendency will be, in the long run, for the Hydras to collect in the localities most frequented by their prey. It is impossible to study an aquarium well stocked with the two animals without being struck by the immense advantage secured to the Hydras by their position on the illuminated side near the surface. In this region the Crustacea often swim in swarms, darting about through a forest of outstretched Hydras, many of which are gorged with food and actively budding, while in other parts of the aquarium both animals are far less abundant. The power of seeking the light, or of avoiding it when too strong, thus confers upon the blind, sluggish Hydra a means of pursuing and capturing its active and highly organized prey, and a vague, diffused sensibility to light becomes in this way of vital importance to its possessor, and may be brought under the action of natural selection. It cannot be doubted that individuals possessing a sensibility higher than the average will have a distinct advantage over the others, so that natural selection will tend to perpetuate them. An interesting feature of the case is that the increased food supply directly increases the rate of reproduction,—*i. e.*, by budding,—so that, in the long run, individuals of high sensibility will multiply more rapidly than those of low sensibility, and leave a larger number of descendants in increasing proportion from generation to generation. It may be noted, further, that the

Lamarckian theory would seem to be inapplicable to this case, for it is impossible to suppose that a Hydra seeks its prey intentionally. It has no means of ascertaining their whereabouts; there is nothing in the character of the movements themselves to indicate that the heliotropic action is conscious or can be increased by individual effort; the heliotropic action is as marked in the complete absence of crustacean food as when it is present. Regarded simply as a useful reflex action which indirectly affects the rate of increase, and which is shown by observation to vary in different individuals, it would seem to be capable of a complete explanation by natural selection alone.

We may now consider the remaining movements. The upward movement towards the surface is performed by both species, but is more active and effective in *H. viridis*. It seems to be not geotropic, but aërotropic (towards the source of oxygen), as indicated by the following experiment. If a large number of Hydras be allowed to collect in the usual position, near the surface, in a small aquarium, and the vessel then be completely filled with water and inverted over a pneumatic trough, the usual relations will be reversed, the air supply coming from below. Under these conditions no definite upward movement takes place, and the contrast with an ordinary open aquarium soon becomes apparent. At first the animals wander indefinitely in all directions. Later they gradually forsake the upper portions of the aquarium, and either crawl downwards towards the lower edge or loosen their attachment and sink to the bottom. The downward movement under these conditions is less definite and rapid than the upward movement under the usual conditions, probably because the supply of oxygen from below is less direct and abundant. The results make it certain, however, that gravity does not determine the movement, and leave little doubt of its aërotropic character. The same conclusion is indicated by the fact that the upward movement is always more pronounced when the water is impure, and when it becomes actually foul the Hydras place themselves at the very edge, actually in contact with the air. Whether the aërotropic movement has been acquired primarily for the sake of respiration, or in order to lead the Hydras more

certainly to their feeding grounds, it would difficult to determine.

We may finally consider the detachment and descent of the Hydras. For a long time, misled by the usual accounts of the feeding habits, I could find no explanation of this movement. The puzzle was solved, however, by the observation that the Hydras, after descending, usually gorge themselves with the sediment at the bottom,[5] sometimes to such a degree that the body seems distended almost to bursting, and the animal remains for a long time torpid and half contracted, often lying prone upon the bottom or hanging down limp and motionless from the side of the aquarium. I have repeatedly observed every stage of this process,—the gathering in of the sediment by the tentacles, its slow ingestion in a great lump, and the ultimate discharge of the innutritious refuse.[6]

Under the microscope the sediment is commonly found to consist of a brownish granular *débris*,—apparently the remains of decayed leaves, etc.,—through which are scattered a few diatoms and numerous minute Infusoria of various species. The sediment is used as food even when the aquarium is abundantly stocked with crustaceans, but under these circumstances the Hydras remain longer at the surface. After the exhaustion of the food-animals—which takes place rapidly when the Hydras become very numerous—the Hydras are compelled to live wholly upon mud, and the cyclical character of the movements becomes more pronounced.

It has been mentioned that the descent of *H. viridis* rarely takes place, and the ingestion of mud by these species has not been observed. This is probably to be explained by the fact that the nutritive processes are aided by the action of the chlorophyll, so that in the absence of crustacean food the advantage of seeking the mud is lessened or counterbalanced by the disadvantage of leaving the illumination most favorable to assimilation. I may

[5] I have observed this habit only in *H. fusca*.

[6] Miss Greenwood states (*Journal of Physiology*, Vol. IX., 1888, p. 349) that Hydra is essentially carnivorous, and that she has never seen the ingestion of inorganic or innutritious matter. In my aquaria, however, *H. fusca* has sometimes subsisted for many weeks with no other visible food supply than the sediment.

add that *H. viridis* is far more hardy than *H. fusca*, being able to live for many days or weeks in foul water that would quickly prove fatal to the latter species. This power of endurance may be due to the liberation of oxygen through the assimilative action of the chlorophyll.

En résumé, the movements of Hydra may be resolved into three actions, which, taken together, insure to the animal a supply of food and air. These are (1) heliotropism, (2) aërotropism, and (3) detachment from the support; and the three are so combined as to form on the whole a cycle. Each movement appears to be called forth by a particular stimulus,—the first by light-rays, the second by dissolved air, the third apparently by diminished food supply of a certain kind. The entire series of movements is useful to the animal, is in large part even of vital importance, and at first sight gives the general impression of consciousness and design; yet a careful analysis of the action weakens this impression, and indicates that it may be regarded as a series of rather complex reflexes, into which the element of consciousness, and *a fortiori* intelligence, need not enter at all.

We may perhaps push the matter a step further back. Granting that the heliotropism of Hydra has been acquired because of the similar heliotropism of Daphnia, we may next seek an explanation of the latter action. The explanation lies close at hand, though I have never seen it stated. There can be little doubt that Daphnia, like Hydra, seeks the light because it there finds the maximum food supply. It is well known that a large number of microscopic green plants possess a considerable power of locomotion, and that they are positively or negatively heliotropic according to the intensity of the light, This is true, for instance, of the zoöpores of numerous species of fresh-water algæ, of many desmids, and other forms. These plants form a part—probably an important part—of the food of Daphnia, and the animal would accordingly gain a great advantage by acquiring a similar heliotropism. Lastly, the heliotropism of the plants is no doubt a provision for placing them in the optimum position for assimilation. It appears, therefore, that the ultimate reason for the heliotropism of Hydra may lie in the mode of assimilation in green plants, and

the case seems to me an interesting one, as illustrating both the correlations between associated organisms, and the nature of the conditions that may enable natural selection to operate at or near the beginning of a series of physiological and morphological modifications.

IV. *Color Discrimination.*—Like many other heliotropic forms, Hydra is chiefly affected by the blue rays. If strips of glass of various colors be fastened to the illuminated side of an aquarium, both species of Hydra show a very marked tendency to collect under the blue, and an equally marked avoidance of the red, green, yellow, or any combination of colors containing no blue. This preference for the blue is (within rather wide limits) independent of intensity. This is strikingly shown by the comparison of a light "yellow" glass with a dark blue cobalt glass,[7] the former being of high, the latter of low, intensity. If equal areas on the light side of an aquarium be covered (see Table II.) (*a*) with yellow, (*b*) with blue, (*c*) with an opaque screen, and a fourth area (*d*) be left uncovered, the result is invariably that in the course of a few days the greatest number of Hydras will be found under the blue (allowance being of course made for the initial differences); the uncovered area stands next, and the shaded and yellow areas contain fewest, with no constant difference between them. That is, the areas compare as follows, as regards:

	Highest.		Lowest.	
Intensity,	(*d*) White,	(*a*) Yellow,	(*b*) Blue,	(*c*) Dark,
Attractiveness,	(*b*) Blue,	(*d*) White,	{ (*a*) Yellow, (*c*) Dark.	

[7] The colors of the glasses used in the experiments, as tested by the spectroscope, were as follows:

Red.—Transmits red and a little orange. Complete absorption of the upper end down to a little beyond the D line. Lower end just perceptibly shortened.

Yellow.—Transmits all but the blue, indigo, and violet. With one layer, complete absorption of upper end down to *b* in the green. Red end very slightly shortened. Two layers cut out of the upper end as far as E, but still transmit some green. Three layers produce nearly complete absorption of the green.

Green.—Transmits green and yellow. Upper end absorbed down to just below F. Red end nearly absorbed, but a faint band transmitted between B and C.

Blue.—Transmits blue, indigo, and violet, and a very little green and red. In a single layer upper end transmitted as far as F. Very faint transmission of green between E and F, and a slightly brighter but narrow band to the left of E. A broad but only barely visible band transmitted in the red. Two layers extinguish the red completely and the green nearly. With three or four layers nothing is visible below F.

The same result is reached if two or even three layers of blue glass are used (see Table II.), although in the last case the blue color is so dark that at a short distance it appears nearly opaque to the eye. It is, moreover, immaterial whether the four (three) areas constitute the only source of light (the top and other sides being in this case covered with black paper) or the diffused light of the room enter from behind and above; the result remains the same. Red and green glass agree nearly with yellow, the Hydras treating them practically as if they were opaque. (This statement will require some modification hereafter.)

The result thus obtained is rendered still more striking if the yellow and blue glasses be interchanged. Within an hour or two the Hydras begin to move out of the yellow light and into the blue, and in a day or two, more or less according to circumstances, the numbers under the blue are far in excess. Thus the Hydras may be driven from one area to another and back again by interchanging the glasses, as often as may be desired (see Table III.). For further details the reader is referred to the explanation of the tables and the chart.

TABLE I.—*Hydra fusca.*

AREAS				I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
ARRANGEMENT OF THE COLORS					Y2		B2		R2		G2	
Date.	*Hour.*	*Weather.*	*Temperature, F.*									
March 9,	10.30 A.M.	Bright.		11	17	19	18	9	27	11	25	16
" 9,	12.30 P.M.	"		10	15	18	19	19	17	24	16	22
" 10,	10.30 A.M.	Cloudy.	67°	14	8	21	22	23	10	27	9	33
" 10,	4.30 P.M.	"	75°	15	7	21	35	24	7	30	7	37
" 11,	9.30 A.M.	"		14	4	23	30	27	9	25	9	32
" 12,	10.30 A.M.	Bright.	74°	21	11	15	34	29	14	28	5	35
" 13,	10.30 A.M.	Cloudy.		26	6	21	41	20	13	33	8	43
" 14,	12.30 P.M.	"	72°	33	8	25	30	31	7	30	5	46
REARRANGEMENT OF THE COLORS					B3		B4		B2		B1	
Date.	*Hour.*	*Weather.*	*Temperature, F.*									
March 15,	9.30 A.M.	Cloudy.	70°	21	16	22	21	21	27	18	25	26
" 15,	3.30 P.M.	Bright.	70°	15	27	15	26	20	30	11	33	26
" 16,	11.30 A.M.	"	62°	17	23	18	22	23	38	15	41	25
" 17,	10.30 A.M.	"	70°	21	25	23	17	27	41	20	47	21
" 18,	11.30 A.M.	"	68°	13	36	20	22	15	43	14	50	18
" 18,	5.00 P.M.	"	68°	13	39	10	21	18	45	14	52	21
REARRANGEMENT OF THE COLORS							Y		G2		R	
Date.	*Hour.*	*Weather.*	*Temperature, F.*									
March 19,	Noon.	Cloudy.	66°			29	7	34	17	39	24	42
" 19,	3.45 P.M.	"				35	6	33	20	38	17	43
" 20,	10.00 A.M.	Bright.	72°			36	10	31	19	33	27	53
" 20,	3.45 P.M.					39	11	35	14	42	21	63
" 21,	9.45 A.M.	Foggy.	70°			33	10	41	13	38	20	65
" 22,	1.00 P.M.	"	66°			35	8	48	17	52	18	64
" 23,	10.00 A.M.	Cloudy.	64°			34	14	33	25	35	24	58

EXPLANATION OF TABLE I.

The areas marked I.–IX. were vertical parallelograms of equal size (34 by 125 mm.), extending from the bottom to the surface, consecutively placed on the side of a large square aquarium, which was placed at a distance of fourteen feet from a window three feet wide and eight feet high, facing the northeast, so that direct sunlight never fell upon the aquarium. The top of the aquarium was covered, the ends and rear side uncovered, so as to admit the diffused light of the room. Area IX. extended to within nine mm. of one end of the aquarium. I. was nearly in the middle. The Hydras had lived for about two months in the aquarium, and were very large and vigorous, many of them actively budding. Throughout the experiment there was a moderate supply of crustacean food, but the animals nevertheless often descended to the bottom and filled themselves with sediment. The alternate areas II., IV., VI., VIII., were first covered with double layers of colored glass (for the color-test see page 421), as in the table, and these were allowed to remain for five days. The results were as follows: The total number of Hydras increased from 153 to 215,—*i.e.*, 40 per cent. The record of the colored areas (taking the mean of the first two and the last two observations) was:

Yellow	decrease (per cent.)		56
Red	"	"	55
Green	"	"	70
Blue	increase	"	92

The record of the light areas was:

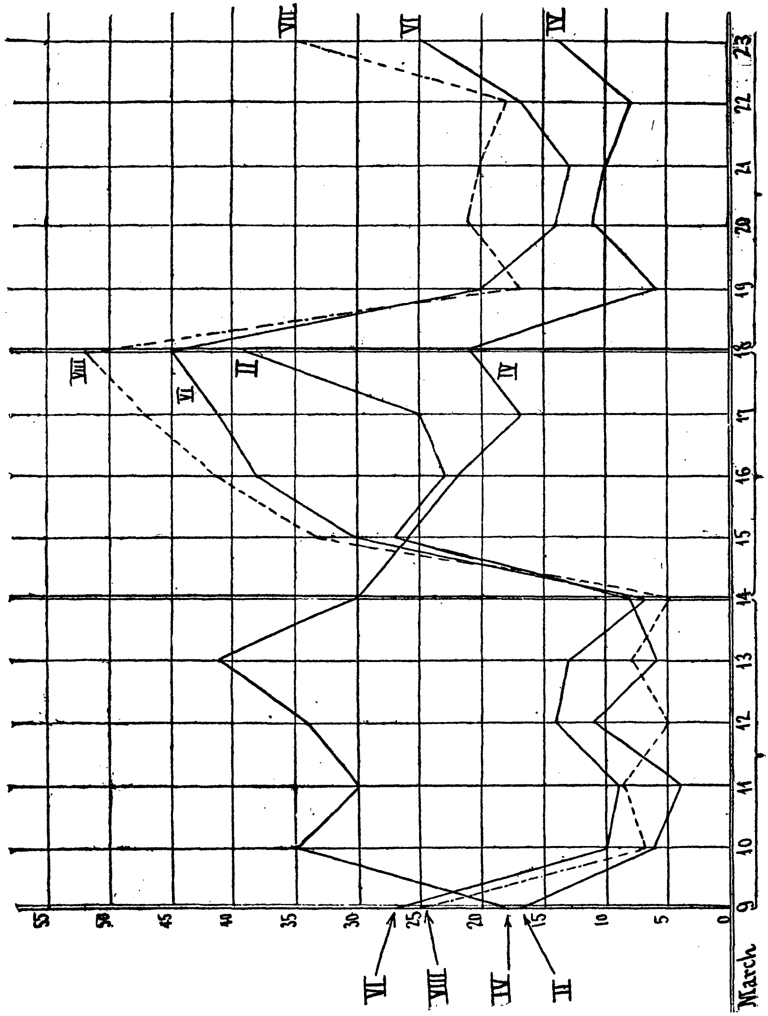
I.	increase (per cent.)		185
III.	"	"	24
V.	"	"	89
VII.	"	"	80
IX.	"	"	134

Thus all of the colors except the blue show a large decrease; the blue and all of the light areas a large increase. The increase in the blue is more than double the general rate of increase, but less than that of the two end areas, I. and IX. The colors are now rearranged, one layer of blue being substituted for the green, two layers of blue for the red, three layers of blue for the yellow, and four layers of blue for the former two layers of area IV. Results, after four days, as follows (taking, as before, the mean of the last two observations):

Total increase 215 to 233,—*i.e.*, eight per cent.			
Single blue (after green), . . .	increase	(per cent.)	692
Double blue (after red)	"	"	340
Triple blue (after yellow) . . .	"	"	436
Quadruple blue (after double blue),	decrease	"	40

Every light area shows a heavy decrease. The experiment seems to show that under the existing conditions the limit of attractiveness, as determined by intensity, lies between three and four layers of blue glass. On replacing the various blues by red, green, and yellow, as in the table, every colored area shows a heavy decrease, and every light area a large increase.

The general result is that, allowing for all variations of weather, temperature, and irregular movements, *H. fusca* shows a very marked "preference" for blue in comparison either with light of other colors or with white light; and an equally marked "preference" for white light as compared with any color except blue.



The above diagram shows in graphic form the same results set forth in Table I. Vertical distances from the base denote the number of Hydras; horizontal distances to the right of the left-hand vertical line denote the date (see Table I.) The colors were changed at the vertical double lines.

The curves show very strikingly, along with the indefinite diurnal fluctuations, the immediate fall in the number of Hydras when placed under any color except blue. The curve IV., as compared with that of II., shows that the attractive influence of blue, under the conditions of the experiment, ceased when the intensity of the blue was diminished beyond three layers of glass.

The comparison of curves II., VI., and VIII. shows a remarkable similarity between them, and indicates that, under the conditions of the experiments, the actions of red, green, and "yellow" did not materially differ.

Explanation of Table II. (page 428.)

This experiment gives a comparison of blue, yellow, white, and the shadow of an opaque screen (II.), and shows the amount of fluctuation from day to day. The general arrangement is the same as in Table I., the same aquarium, Hydras, position, and areas being used as before, but the areas are increased in number, so as to extend over nearly the whole illuminated side, area I. being three mm. from one end, and area XVI. nine mm. from the other. The comparison is made between the first and last observations.

Total increase, 421 to 674,—*i.e.*, 60 per cent.

Blue, increase	327 per cent.
Yellow, decrease	30 "
Dark screen, decrease	37 "
Light (a mean of V., VI., VII., increase	30 "

An inspection of the table shows that although these figures express the broad general result with sufficient accuracy, they are not to be taken to mean more than this, since there is a wide margin of apparently fortuitous variation from day to day. The table shows a marked "preference" for the blue, and a much less marked but still distinct "preference" for ordinary daylight, as compared with the light of diminished intensity behind the opaque screen. The yellow glass acts practically as if it were opaque.

TABLE II.—*H. fusca.*

AREAS	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	XV.	XVI.
ARRANGEMENT			B			L			D					Y		
March 28, 4.30 P.M.	24	14	15	19	26	27	14	22	19	29	24	33	29	34	32	60
" 29, 10.30 A.M.	24	14	29	11	25	26	16	25	16	29	25	29	31	17	45	62
" 29, 4.00 P.M.			28			29			15					22		
" 30, 9.45 A.M.	17	13	28	13	24	22	25	24	16	29	27	34	34	12	50	73
" 31, 9.30 A.M.	23	13	34	16	22	29	22	30	10	24	33	34	34	16	47	84
April 1, 10.00 A.M.	21	21	34	12	26	27	17	30	14	23	29	34	31	24	55	65
" 2, 11.00 A.M.	18	17	42	19	30	23	22	30	14	22	24	27	43	24	54	73
" 3, Noon.	19	26	42	23	32	27	20	14	19	21	29	31	35	23	53	83
" 4, 10.00 A.M.	14	22	46	25	37	33	14	26	11	19	33	31	45	17	46	78
REARRANGEMENT			B2						D					G2		
April 4, 1.00 P.M.			52						10					22		
" 4, 4.00 P.M.			56			34			7					21		
" 4, 8.00 P.M.			54						9					24		
" 5, 10.00 A.M.	21	29	49	28	44	35	17	27	15	18	29	38	47	28	54	77
			B3													
" 5, 4.00 P.M.			50			36			13					24		
" 6, 10.00 A.M.	15	39	46	28	39	41	23	38	6	22	23	28	50	19	45	88
			B4													
" 8, 1.00 P.M.	37	43	38	32	50	39	30	41	9	25	24	38	37	23	53	100
														Y		
" 9, 4.30 P.M.	40	50	34	37	48	39	33	44	11	21	23	35	44	17	71	83
			B3													
" 10, 9.30 A.M.			49			46			9					18		
" 15, 11.00 A.M.	59	52	64	17	25	30	33	43	12	33	31	33	43	24	81	94

TABLE III.—*Hydra viridis.*

Areas	I.	II.	III.	IV.	V.	VI.	VII.
Arrangement	G		B		Y		R
March 24, 5.30 P.M.	1	0	6	2	8	2	2
" 24, 8.30 P.M.	1	1	7	6	5	5	1
" 25, 11.45 A.M.	0	0	14	0	0	7	0
Rearranged	G.		Y		B		R
March 25, 2.00 P.M.	0	3	4	5	5	4	0
" 25, 5.00 P.M.	0	5	1	6	6	4	0
" 26, 5.00 P.M.	0	7	3	3	6	6	0
" 27, 4.00 P.M.	0	3	0	4	9	6	2
" 28, 4.00 P.M.	0	3	0	5	9	6	2
" 29, 3.00 P.M.	0	3	0	2	15	4	0
Rearranged	G		Y		R		B
March 29, 9.45 P.M.	0	4	0	9	6	8	2
" 30, 9.45 A.M.	0	4	0	10	1	6	8
" 31, 9.00 A.M.	0	4	0	12	0	5	9
Rearranged			B.		B		
March 31, 12.30 P.M.	1	1	7	4	6	6	4
April 1. 9.30 A.M.	5	1	11	2	9	4	4
Rearranged			B2		B1		
April 2, 10.00 A.M.	5	5	10	0	13	7	6
" 2, 9.00 P.M.	3	2	7	2	19	2	6
" 3, 11.00 A.M.	6	3	3	5	14	6	5

Explanation of Table III.

General conditions of the experiment, as in Tables I., II., but the animals were in a cylindrical aquarium, eight inches in diameter, and the areas were much smaller (colored areas, 20 by 70 mm.; light areas, 10 by 70 mm.). The middle area (IV.) was turned towards the window. The end areas (I., VII.) would therefore tend to receive any Hydras advancing towards the light around the sides.

The results show a complete avoidance of all colors except blue, and a marked "preference" for blue as compared with ordinary daylight.

The results obtained by the use of colored glasses are confirmed by tests with the actual spectrum.[8] If a spectrum produced by passing a beam of light from an Argand lamp through a prism be thrown upon a group of Hydras, they show a very marked tendency to collect in the lower blue. It is

[8] For this purpose I have used an Argand gas-burner, the light from which was passed first through a narrow slit, then through a biconvex lens to render the rays approximately parallel, and finally through a large prism (bisulphide bottle). The spectrum thus obtained was projected upon the side of a square aquarium ruled in small squares, and at

difficult to fix exactly the limit of the attractive rays. As nearly as can be determined they extend over the lower third of the blue end,—*i. e.*, from G nearly to F,—and for a short distance into the green.

The results of these experiments leave no doubt that, irrespective of intensity, Hydra prefers[9] blue light to all other colors and to white light (ordinary daylight). My observations indicate further that, although the blue rays are by far the most efficient, a slight attractive influence is also exercised by the green. Under ordinary circumstances—*i. e.*, when diffused daylight is not cut off from behind or above—Hydra appears to be as indifferent to green as to red or to an opaque screen. If, however, the animal be enclosed in an aquarium so arranged as to offer it the choice between green and either red or "yellow," a distinct though slight preference is shown for the green, and the animals very gradually accumulate behind it. The green glass used in this experiment shows no trace of blue under the spectroscope. If the choice be offered between red or "yellow" (the latter = red + yellow + green), no perceptible preference is shown, even if the experiment be continued for weeks. This result is of some interest, for it seems to show that the slight attractive influence of green is nullified by the admixture of red and yellow, just as the attractiveness of blue is diminished by the admixture of the other colors, as has been shown.

The preference of Hydra for blue as compared with white light is a very remarkable fact; for the animal can never have had any experience of pure blue, but only of white, light,—*i. e.*, blue plus the other colors of the spectrum. Neither can the preference for blue glass be due simply and solely to the attractive influence of the blue rays, for the ordinary daylight entering the aquarium contains at least as many blue rays as the same

the distance adopted (about two feet from the prism) was about three inches in length. The apparatus was placed in a perfectly dark underground room, and every pains was taken, by the use of suitable screens, etc., to exclude from the aquarium all light excepting that proceeding from the prism.

[9] The word "prefer" is perhaps objectionable as implying an act of consciousness on the part of Hydra. I do not wish to make such an implication, however, and use the word only for the sake of brevity.

light after its passage through the blue glass. The conclusion would seem to be inevitable that the lower rays exercise an injurious or repellant action, and thus tend to produce negative heliotropism, or to counteract the effect of the blue rays. It is a tempting hypothesis to suppose that the blue rays are most efficient in light of low intensity, and the lower rays most efficient in high,—a view which would explain in the clearest manner the reversal of heliotropism with the change in intensity. Experiment, however, does not sustain this conclusion, but indicates that the animal is wholly indifferent to the lower rays. Hydras supplied only with light that has passed through red or yellow glass do not noticeably move either away from or towards it, but behave as though the glass were opaque. Tested with the actual spectrum, they appear to be quite indifferent to all of the rays except the lower blue and the upper green. I have also tested this question by the comparison of nearly pure blue glass with purple (aqueous solutions of methyl-violet of various intensities), which is a mixture of blue and red. Any repellant action on the part of the red might reasonably be expected to counteract more or less completely the attractiveness of the blue. Experiment shows, however, that purple is as attractive as pure blue, —neither more nor less, as far as can be determined.

It appears, therefore, to sum up, that although the lower rays are without any perceptible action on Hydra, by themselves or when mixed singly with the upper rays (as in purple), yet they partially counteract the attractiveness of the blue rays when mixed with them as they are in ordinary daylight, and of the green rays when mixed with them so as to form yellow (*i. e.*, white light minus blue). This paradoxical result I am at present unable to understand, but the problem is undoubtedly worthy of the most careful investigation.

Why the blue-green rays alone should be operative it is impossible to say. The recent works of Loeb and Groome upon animal heliotropism, and the earlier work of Sachs, de Bary and others upon plants, show that in all probability the blue rays are the effective ones in all cases of heliotropic action, whatever its purpose or mode of origin, whether in plants or animals, whether

guided by differentiated visual organs or not. If this conclusion be well founded, the efficiency of the blue rays must depend upon some fundamental characteristic of protoplasmic action, and the sensibility to the lower rays, as manifested by differentiated visual end-organs in higher forms, has probably been secondarily acquired by an extension of the original blue-sensibility.

It seems hardly necessary to point out that this conclusion by no means implies that all forms of heliotropic action have the same physiological meaning. It relates solely to the *mode of stimulus*, not to the purpose of the actions called forth by the stimulus. Sneezing and winking may both be produced by a sudden visual stimulus, but we do not for this reason conclude that these actions must play the same physiological *rôle*.

To the ultra-violet rays the animals, as far as can be determined, are as indifferent as to the ultra-red.

V.—The last point to be considered relates to the mode in which the stimulus acts,—a question of greater importance than appears at first sight. There seems to be no doubt that blue rays impinging upon Hydra exert a directly attractive influence; for if an aquarium be supplied with blue light only (entering through a small window) the animals move pretty directly towards it, and do not simply wander aimlessly about until they reach the blue by accident. The case is different when a number of the animals, already situated on the illuminated side of a square aquarium, are offered the choice between a number of differently colored slips fastened to that side.

Under these conditions, as has been shown, the animals decrease under the red, yellow, and green glasses, and steadily accumulate under the blue, although no unmixed blue light impinges upon those individuals not actually behind the blue glass. The lower rays, however, exert no repellant action in themselves, and we must therefore assume that the animals tend to wander irregularly about until the blue areas are accidentally discovered. Observation shows, moreover, that the tendency to wander exists under every condition of illumination. By marking off the side of an aquarium into small squares it is easy to follow and accurately record the individual movements of a group of Hydras for

a long time. The results show that even after the animals have thoroughly established themselves in the usual position on the illuminated side they are to some extent continually on the march, and seldom remain in one spot more than a day or two, and the time is usually much less than this. I cannot make out that the movements are more active under the red, yellow, or green, or in darkness, than in daylight or under blue, though a *sudden change*, whether of color or of intensity, is apt to stimulate the movements for a time. This latter fact probably explains the comparatively rapid dispersal of the animals upon the substitution of a neutral color for blue (see tables), which at first sight seems to point to a direct repellent action.

On the whole, the facts seem to warrant the conclusion that Hydra has an innate (automatic?) tendency to wander, and that light and oxygen operate not so much by calling forth new movements as by the modification of indefinite movements that tend continually to recur irrespective of external stimuli. If this be so, the case shows an interesting analogy to the movements of plants, many of which (including heliotropism), as Darwin has so strikingly shown, have arisen through the modification by special stimuli of an innate circumnutatory movement. Some of these movements in plants, though no doubt unconscious, have an extraordinary likeness to purposive, intelligent acts. It would be difficult to say in what lies the superior claim of Hydra to recognition as a conscious, not to say intelligent, being.

Bryn Mawr, Pa., April, 1891.